

Habitat associations of old forest bird species in managed boreal forests characterized by forest inventory data

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Conservation areas are important for many species associated with old forests, but most individuals still occur in commercially-used forest landscapes. We conducted three-visit breeding bird surveys in a total of 37 study squares of 1 km², and used National Forest Inventory data to evaluate habitat associations of birds linked with old forests in three geographical regions: southern, eastern and northern Finland. All study squares were located within managed forests. Out of the total of 23 pre-selected old-forest species, 12 were recorded in the study squares of all three study regions; the number of species varied between 16 and 21 among the regions. The total abundance did not significantly vary among the regions, but the abundances of many single species varied significantly among the regions. Forest-patch size was the single most important factor, positively affecting the abundance of most of the species considered. Development class affected most species in the south and east, and species associated with mature and old forest stands in general. Tree height and stand age were included into the models more often than tree species and diameter. In general, forest patch size, developmental class, age and tree height were among the most important factors in explaining the abundance of old-forest bird species in commercially-used forests. These stand characteristics appeared particularly important for resident species and cavity nesters. Our results indicate that the responses of old-forest bird species to environmental variation in managed, forested landscapes are individualistic, and different factors may affect them in different regions. Variables included in the patch-level forest-inventory data well explained abundance variation of species associated with old forests. Our results underscore the importance of integrating national forest-inventory and bird-survey data to obtain information about species habitat requirements and forest-sector related information about the effects of forestry on birds.



1. Introduction

Loss of habitat and large-scale fragmentation of forests are considered the most serious factors threatening global biodiversity (e.g., Barbault & Sastrapradja 1995). Most boreal forests have been converted to commercial use (e.g., Forman & Godron 1986, Gustafsson & Parker 1992, Virkkala *et al.* 2000), and consequently several hundreds of species requiring natural boreal forests have become threatened or locally extinct, particularly many so-called old-growth forest specialists (Esseen *et al.* 1997, Rassi *et al.* 2001, Gärdenfors 2005). Natural boreal forests have many structural and spatial components and processes that are lacking or altered in managed forests, such as very old trees, cavity trees, a well-developed understorey of tree saplings and shrubs, uneven age structure of trees, and post-fire succession (Esseen *et al.* 1997).

Recent studies have linked habitat structure and composition, as well as landscape structure, to changes in animal populations, which have implications to reserve planning and management practices (Edenius & Elmberg 1996, Jokimäki & Huhta 1996, Elmberg & Edenius 1999, Saab 1999, Villard *et al.* 1999, Fuller *et al.* 2007, St-Laurent *et al.* 2007). Conservation areas are important refuges for many old-forest bird species (Virkkala & Rajasärkkä 2007), but they are not islands that lack interactions with the surrounding matrix (Janzen 1983, Väisänen *et al.* 1986). As the proportion of protected areas is small relative to the total land area, management of the surrounding areas appears especially important.

The steep decrease in natural forest area due to intensified forestry is clearly reflected in bird abundances. In Finland, for instance, during recent decades most species increasing in abundance are associated with younger stands, while the bulk of threatened or declining forest-bird species prefer the oldest age classes of forests (Järvinen *et al.* 1977, Järvinen & Väisänen 1978, 1979, Väisänen *et al.* 1998, Rassi *et al.* 2001). In order to support viable populations of old-forest species, we need more information about the demography of these species, especially in commercially used forests.

Generally, the richness of forest birds within landscapes is lower the heavier the impact of forestry (Edenius & Elmberg 1996) and the most im-

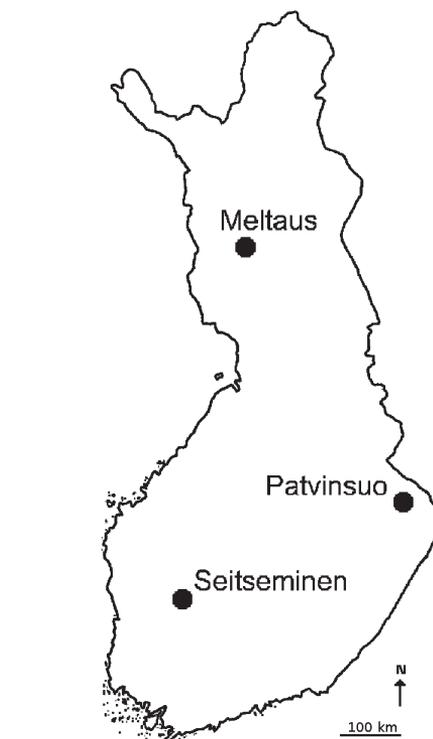


Fig. 1. The study regions: Seitsemien (south), Patvinsuo (east) and Meltaus (north).

portant features of forests for birds include size, age, and the distribution of patches suitable for nesting or other essential activities (Haapanen 1965, 1966, Helle 1985a, Virkkala 2000). In addition, landscape-level factors such as fragmentation can have pronounced effects on birds (McLellan *et al.* 1986, Wilcove *et al.* 1986, Opdam 1991, Andrén 1994, Bellamy *et al.* 1996, Jokimäki & Huhta 1996, Esseen *et al.* 1997, Schmiegelow *et al.* 1997, Kouki & Väänänen 2000, Mönkkönen *et al.* 2000). Different tools have been developed to assist retaining biodiversity in managed forests. To use birds to assess the effectiveness of forest management and planning policy, and that of operational forest management, information about the habitat needs of individual bird species is needed.

In the present study, we examined habitat associations of a set of a priori selected species that prefer mature and old forests by three-visit square surveys in southern, eastern and northern Finland. We evaluated three topics. Firstly, we compared the abundance of these species in managed forests among the three regions. Secondly, we investi-

gated how well the National Forest Inventory data (NFI; VMI in Finnish; forest structural characteristics at the forest-patch level over the whole country), collected by the Finnish Forest Research Institute (METLA), predicts the abundance of old-forest bird species. Thirdly, we studied if there are specific forest patch characteristics that are important for all or most of the study species, and if the same factors affect species independently of the study region. As our study sites were located in state-owned areas, the collected bird data could be directly linked to the NFI variables, which is important from both conservation and forestry-sector points of view (Edenius & Mikusiński 2006, Fearer *et al.* 2007, St-Laurent *et al.* 2007, Venier & Pearce 2007). An integration of national bird-monitoring and forest-inventory data are a promising way to obtain information about the relationship between bird species and habitat characteristics across large spatial scales (cf. Fearer *et al.* 2007).

2. Material and methods

2.1. Study areas

The fieldwork was conducted on state-owned, mainly commercially-used forests in three regions: Seitsemien (southern Finland; 61°N, 23°E), Patvinsuo (eastern Finland; 63°N, 30°E), and Meltaus (northern Finland; 66°N, 25°E; Fig. 1). A number of 1 x 1 km study squares of the Finnish ordnance survey uniform grid system were established in each study region (10 for both Seitsemien and Meltaus, and 17 for Patvinsuo). The distance between the individual study squares ranged ca. 0–6 km in Seitsemien, 0–8 km in Patvinsuo, and 0–33 km in Meltaus.

The study squares were situated within large, continuous forest areas for which NFI data were available a priori and could be directly integrated into our bird-survey data. These squares represented common forest environments within the three regions and were selected so that the proportion of environments other than forests was as low as possible (less than 10%). Although the study squares were intended to represent various kinds of forests occurring within the three regions, the proportion of older age classes of forests was low

even in the study squares situated within national parks. Hence, here “national park” does not refer to “old forest”. We use the term old forest to refer to forests with dominant trees at least 50 years old, and including many characteristic, natural old-growth forests. In the present study, stands of old forests were relatively small even for study squares within national parks. So, the effect of these parks *per se* on our bird data should be minor for up to a distance of several kilometres (cf. Brotons *et al.* 2003).

2.2. NFI data

We used NFI data (forest-patch and tree characteristics within a given patch) based on field measurements collected by METLA. These data were extracted from the database of Metsähallitus (the Finnish Forest and Park Service, the manager of state-owned lands in Finland) for the spatial scale of individual forest patches. Forest-patch characteristics included patch size, development class, vegetation class and tree-species dominance (Table 1). Development classes included (1) clearings, (2) sapling stands, (3) young regenerating stands, (4) mature regenerating stands, (5) mature stands, and (6) old forest stands. In this paper, “old forests” refers to development classes 4–6, and the proportion of these forests in different regions varied between 10% and 37% (Table 1). Vegetation classes were (1) rocks, (2) barren heaths, (3) dry heaths, (4) partly dry heaths, (5) moist heaths, and (5) rich herb forests. Dominant tree species were mostly conifers, Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) Karst. Some forests included mixtures or were dominated by deciduous trees (*Betula*, *Populus* and *Alnus*). Variables characterizing the trees within each forest patch included species, average age, height and diameter.

Bird–habitat relationships were examined in those forest patches that covered most of the area of individual territories. Therefore, the habitat data occasionally covered also some patches that were outside the study-plot perimeter. The corresponding NFI data were obtained from approximately 0.99–1.30 km². However, the largest patches not adequately covered by bird surveys were excluded.

Table 1. Structural characteristics of managed forests of Seitsemien, Patvinsuo and Meltaus regions. Forests of developmental stage ≥ 4 (at least 50 years of age) are considered old. Development class includes forests from clear-cuts to old forests, and vegetation class covers habitat types from rocky to herb-rich forests. Dominant tree species were Scots pine and Norway spruce; mixed-species and deciduous forests were the other dominants.

Variable	Seitsemien (south)	Patvinsuo (east)	Meltaus (north)
N of patches	513	625	276
N of patches studied	396	560	226
N of old forest patches	105	73	60
Total area studied (ha)	1,201.4	2,533.1	2,070.0
Percentage of old patches	26.5	13.0	26.5
Area of old forests (ha)	447.9	260.2	515.6
Percentage of old forests	37.3	10.3	24.9
Development class (median)	Young forest	Young forest	Sapling stand
Vegetation class (median)	Partly dry heath	Partly dry heath	Partly dry heath
Dominant tree species (median)	Pine	Pine	Pine
Patch size ($x \pm SD$; ha)	2.8 ± 4.1	4.7 ± 6.5	10.4 ± 16.0
Stand age ($x \pm SD$, years)	66.3 ± 43.6	49.5 ± 44.5	76.1 ± 69.0
Tree height ($x \pm SD$, m)	12.8 ± 6.9	8.7 ± 7.5	9.2 ± 6.1
Tree diameter ($x \pm SD$, cm)	17.1 ± 9.9	10.8 ± 9.8	11.8 ± 10.5

In all study regions, stand age, tree height and tree diameter were positively correlated with each other ($P < 0.001$ in all cases). In addition, the following statistically significant correlations (all with $P < 0.001$) were observed in Seitsemien: patch size and development class (+ = positive interaction), development class and vegetation class (– = negative interaction), development class and dominant tree species (+) and vegetation class and dominant tree species (–) were correlated. Moreover, in Patvinsuo, patch size and development class (+), patch size and dominant tree species (–), development class and dominant tree species (+), vegetation class and dominant tree species (–), vegetation class and tree height (–), and vegetation class and tree diameter (–) were correlated. Stand size and vegetation class (+) and development class and dominant tree species (+) were correlated in Meltaus.

2.3. Bird surveys

Because an accurate and comprehensive census of the forest-bird fauna needed for a detailed monitoring program would be time consuming and expensive, we studied a predetermined group of relatively sparse bird species that are known to prefer old or mature forests (Table 2). The selection of

species was based on von Haartman *et al.* (1963–1972) and Väisänen *et al.* (1998). These species prefer maturing or mature forests, though some occur in younger forests as well (e.g., Väisänen *et al.* 1998, Kouki & Väänänen 2000, Mönkkönen *et al.* 2000, Jansson 2001, Virkkala & Rajasärkkä 2001). By excluding common species, the total effort could be efficiently directed to sparsely-distributed species that are often more sensitive to habitat alterations than common ones (Solonen & Jokimäki 2011). Wide-ranging species, such as birds of prey, were excluded because observations of these species could not be meaningfully linked to the habitat data at the spatial scale considered (i.e., stand level).

A single-visit method detects about 60% of breeding pairs and 90% of species in forested areas (Järvinen & Lokki 1978, Kissling & Garton 2006). According to Koskimies & Väisänen (1991), if a single-visit survey is desired, it should be conducted around midsummer. Such a monitoring scheme may not reliably reflect the abundance and distribution of scarce species, in particular early-breeding residents (Solonen & Jokimäki 2011). Therefore, we used a modification of the so-called summer atlas protocol (Pakkala & Väisänen 2000, 2001, Solonen & Jokimäki 2011). According to this protocol, the study squares were explored for the preselected species three times during the

Table 2. Mean densities (territories/km²) ± SD of 23 forest-bird species for Seitsemien, Patvinsuo and Meltaus, based on 1 km × 1 km study-square surveys conducted in 2004. Number following the region name shows the number of study squares. Species-name abbreviations are used in Table 3. Numbers in parentheses show mean densities observed in protected forests in Finland in corresponding areas (data from Virkkala & Rajasärkkä 2007). Kruskal-Wallis χ^2 test was performed to evaluate the similarity of the regions, with subsequent Tukey pair-wise tests. Statistically significant differences (here, $P < 0.001$) are indicated by letters: M = Meltaus, P = Patvinsuo, and S = Seitsemien.

Species	Abbr.	Seitsemien; 10	Patvinsuo; 17	Meltaus; 10	χ^2	P	Tukey
<i>Bonasa bonasia</i>	Bonbon	0.85 ± 0.99 (1.43)	2.91 ± 2.66 (1.10)	1.42 ± 1.15 (0.93)	5.02	0.081	
<i>Lagopus lagopus</i>	Laglag	– (0)	0.21 ± 0.46	0.74 ± 0.63	29.11	<0.001	M > S, P > S
<i>Jynx torquilla</i>	Jyntor	0.19 ± 0.28 (0.13)	0.32 ± 0.53 (0.10)	0.67 ± 1.03 (0.08)	1.64	0.441	
<i>Dendrocopos major</i>	Denmaj	1.87 ± 1.22 (1.59)	2.74 ± 1.35 (2.22)	2.42 ± 2.15 (1.40)	1.79	0.409	
<i>Picooides tridactylus</i>	Pictri	0.28 ± 0.38 (0.14)	0.15 ± 0.22 (0.28)	0.19 ± 0.28 (0.53)	1.28	0.529	
<i>Bombycilla garrulus</i>	Bomgar	– (0)	0.53 ± 0.58 (0.08)	2.70 ± 1.34 (0.35)	30.09	<0.001	M > S
<i>Troglodytes troglodytes</i>	Trotro	0.14 ± 0.13 (0.83)	0.44 ± 1.03 (0.62)	– (0.14)	30.13	<0.001	P > M, S > M
<i>Phoenicurus phoenicurus</i>	Phopho	0.84 ± 0.88 (1.18)	4.50 ± 2.73 (3.78)	8.50 ± 2.64 (4.92)	23.93	<0.001	M > S
<i>Turdus viscivorus</i>	Turvis	1.14 ± 1.06	1.71 ± 0.97	1.12 ± 0.71	3.04	0.219	
<i>Phylloscopus trochiloides</i>	Phydes	0.19 ± 0.28 (0.25)	0.28 ± 0.36 (0.33)	– (0.07)	27.92	<0.001	P > M, S > M
<i>Phylloscopus sibilatrix</i>	Physib	0.19 ± 0.28 (5.92)	0.12 ± 0.10 (2.60)	– (0.23)	31.74	<0.001	S > M, P > M
<i>Phylloscopus collybita</i>	Phycol	2.02 ± 1.74 (1.28)	0.82 ± 1.05 (0.43)	– (0.12)	24.79	<0.001	S > M, P > M
<i>Ficedula parva</i>	Ficpar	0.19 ± 0.28 (0.21)	0.26 ± 0.50 (0.10)	– (0.02)	26.97	<0.001	P > M, S > M
<i>Ficedula hypoleuca</i>	Fichyp	2.93 ± 2.52	2.87 ± 2.67	2.20 ± 1.93	0.57	0.751	
<i>Parus montanus</i>	Parmon	3.20 ± 1.32	7.00 ± 2.24	2.28 ± 1.87	21.65	<0.001	P > M
<i>Parus cinctus</i>	Parcin	– (0)	– (0)	0.84 ± 0.88 (0.44)	35.05	<0.001	M > P, M > S
<i>Parus cristatus</i>	Parcri	4.20 ± 1.32 (3.62)	3.82 ± 1.89 (2.85)	– (0.35)	22.11	<0.001	S > M, P > M
<i>Parus caeruleus</i>	Parcae	0.95 ± 1.16	–	–	35.02	<0.001	S > M, S > P
<i>Parus major</i>	Parmaj	2.70 ± 1.70	3.31 ± 3.02	0.67 ± 0.92	10.25	0.006	
<i>Certhia familiaris</i>	Cerfam	2.02 ± 1.46 (2.54)	0.49 ± 0.97 (1.61)	0.38 ± 0.64 (0.64)	12.03	0.002	
<i>Perisoreus infaustus</i>	Perinf	– (0)	0.15 ± 0.22 (0.10)	0.93 ± 0.70 (0.86)	30.31	<0.001	M > S, M > P
<i>Pyrrhula pyrrhula</i>	Pyrpyr	2.26 ± 1.86	4.42 ± 2.89	1.91 ± 1.27	5.92	0.052	
<i>Emberiza rustica</i>	Embrus	0.56 ± 0.66 (0.82)	1.11 ± 1.40 (2.21)	0.56 ± 0.66 (3.07))	1.17	0.558	
Total territory density		26.72 ± 8.71	38.2 ± 14.47	27.72 ± 6.88	5.87	0.053	
Number of species		19	21	16			

breeding season in 2004: in April–May, in the first half of June, and mid-June. In each census, the study squares were thoroughly studied, spending at least five hours per square. All records of preselected species were spatially-referenced to a forest map. The groups of records or clearly separate single observations of resident individuals that displayed activities associated with breeding (such as singing, alarm calling or feeding chicks) were interpreted to indicate territories, following broadly the territory-mapping protocol (e.g., Bibby *et al.* 1992). The location of a given territory was indicated either by the location of the observed nest or by the centre of the observations interpreted to indicate a territory, and the location of each territory was linked to corresponding forest-patch (NFI) data. Because the interpretation of territories involves subjectivity, all territory interpretations

were made by the author TS. The field work was conducted by two persons in Seitsemien, two persons in Patvinsuo and one person in Meltaus. To avoid differences in the skills of observers to introduce heterogeneity in abundance estimates, the data were collected only by experienced observers with about 10–20 years' experience in bird census work.

2.4. Statistical methods

We used Kruskal-Wallis test to compare the abundance of birds between different study regions. In these analyses, the dependent variable was bird density per study square (territories/km²) for each study region. We made paired comparisons with Tukey non-parametric a posteriori test (Zar 1984)

at $P < 0.001$. This lower-than-standard alpha level was applied to avoid misleading interpretations.

Habitat relationships of the a priori selected species were first analyzed by GLM univariate analysis of variance. Because the interactions between study location and the other variables affected the abundance of the most species, we made separate analyses for different regions using a stepwise multiple regression. Here, the P value for entering variables into models was set to < 0.05 and for removing variables was set to < 0.10 . A constant was included in the equations. Two separate analyses were conducted by first using general forest-patch variables (patch size, development class, vegetation class and tree-species dominance), and by subsequently using variables describing trees within each forest patch (tree species, and average age, height and diameter of canopy trees). Of these, patch size was continuous, and development class, vegetation class and species dominance were categorical, variables. The number of territories of each bird species in each habitat patch was the dependent variable. Because we were interested in the possibility for the existence of specific forest characteristics important for all or most study species, and if the same factors affect bird species independently of study region, we separately modelled each species for each study region. Systat (Systat Inc. 2004) and SPSS (SPSS Inc. 2006) software were used in the analyses.

3. Results

3.1. Bird species composition and abundances

Each of the 23 focal species were observed in some of the study regions (Table 2). The total density (territories/km², or territories/study square) of birds did not differ between regions but the densities of many species varied significantly among them. Some species occurred only in the north or were more abundant in the north than in the south, such as Willow Grouse (*Lagopus lagopus*), Waxwing (*Bombycilla garrulus*), Siberian Tit (*Parus cinctus*) and Siberian Jay (*Perisoreus infaustus*). On the other hand, some species were observed only in the south or their densities were higher there, such as Wren (*Troglodytes troglodytes*),

Greenish Warbler (*Phylloscopus trochiloides*), Wood Warbler (*P. sibilatrix*), Chiffchaff (*P. collybita*), Crested Tit (*Parus cristatus*) and Blue Tit (*P. caeruleus*). Regional densities were relatively similar in the Wryneck (*Jynx torquilla*), Great Spotted Woodpecker (*Dendrocopos major*), Three-toed Woodpecker (*Picoides tridactylus*), Mistle Thrush (*Turdus viscivorus*), Pied Flycatcher (*Ficedula hypoleuca*) and Rustic Bunting (*Emberiza rustica*).

3.2. Effects of forest-patch characteristics

Multiple regressions revealed that, irrespective of region, the abundance (territories/patch) of most species was positively correlated with patch size (Table 3). Development class significantly affected the abundance of most species in Seitsemien and Patvinsuo (south and east, respectively), but in Meltaus (north) it was an important factor only for the Great Spotted Woodpecker. All the focal species were more abundant in older age classes of forests.

Vegetation class affected the abundance of Chiffchaff and Rustic Bunting in Patvinsuo (east), and Redstart (*Phoenicurus phoenicurus*) in Meltaus (Table 3). Tree species dominance affected the abundance of only Great Tit (*Parus major*) in Seitsemien, whereas four species (Hazel Grouse *Bonasa bonasia*, Three-toed Woodpecker, Chiffchaff and Red-breasted Flycatcher (*Ficedula parva*) were affected in Patvinsuo, and four species (Hazel Grouse, Willow Tit *Parus montanus*, Pied Flycatcher and Rustic Bunting) were affected by vegetation class in Meltaus. All of these species had peak abundances in spruce-dominated or mixed forests located in moist heaths or rich herb forests.

3.3. Effects of tree characteristics within forest patches

Stand age (19 cases) and tree height (15) were included into the models more often than tree species (5) and tree diameter (3; Table 3). The abundance of Hazel Grouse, Bullfinch (*Pyrrhula pyrrhula*), Great Spotted Woodpecker, Three-toed Woodpecker, Wren, Willow Tit, Crested Tit, Great Tit,

Table 3. Stepwise linear regression models for species–habitat relationships. Separate analyses were conducted for forest-patch characteristics and tree characteristics within forest patches of different study regions. “No model” = no variables were entered into the model; # = the species was not observed in the given region. Partial R^2 for each variable is given in parentheses. Statistical significances are indicated as *** ($P < 0.001$), ** ($P < 0.01$) and * ($P < 0.05$). “–” after a variable denotes a negative relationship. For species abbreviations, consult Table 2. Positive relationship with tree dominance indicates that a species prefers deciduous over coniferous forests, positive relationship with development class indicates that a species prefers mature or old-growth forests over younger development phases, and positive relationship with vegetation class indicates that a species prefers herb-rich over drier forests.

Species	Patch characteristics			Tree characteristics		
	Seitsemäen	Patvinsuo	Meltaus	Seitsemäen	Patvinsuo	Meltaus
Bon bon	Patch size (10.0)***	Patch size (7.3)*** Tree dom. (2.1)***	Patch size (21.1)*** Tree dom. (1.7)*	No model	No model	Tree height (1.4)*
Lag lag	#	Patch size (0.8)*	No model	#	No model	No model
Jyn tor	No model	No model	No model	No model	Age (0.4)*	No model
Den maj	Patch size (11.5)*** Dev. class (1.2)**	Patch size (9.6)*** Dev. class (1.7)***	Patch size (9.5)*** Dev. class (2.7)**	Tree height (1.1)*	Age (0.7)**	No model
Pic tri	Patch size (27.9)***	Patch size (1.0)* Tree dom. (1.0)*	No model	No model	Age (1.4)***	Tree height (1.4)**
Bom gar	#	Patch size (3.8)***	Patch size (17.3)***	#	No model	No model
Tro tro	No model	Dev. class (0.1)*	#	No model	Age (3.1)*** Tree diameter –(0.7)** Tree height (0.4*)	#
Pho pho	Patch size (1.9)*** Dev. class –(0.7)*	Patch size (4.6)*** Dev. class (4.5)***	Patch size (37.9)*** Veg. class (1.5)**	Tree height –(2.0)***	Age (3.1)*** Tree species –(0.3)**	Tree species –(1.6)**
Tur vis	Patch size (20.6)*** Dev. class (1.1)**	Dev. class (3.2)*** Patch size (2.8)***	Patch size (8.7)***	Age (1.8)***	Tree height (2.5)***	No model
Phy des	Patch size (0.9)*	Dev. class (0.8)*	#	Age (1.4)***	No model	#
Phy col	Patch size (19.8)*** Dev. class (3.4)***	Tree dom. (1.5)*** Patch size (1.7)*** Veg. class –(0.7)* Dev. class (0.7)*	#	Age (2.4)***	No model	#
Phy sib	No model	No model	#	No model	Tree height (0.6)*	#
Fic par	No model	Tree dom. (1.9)*** Patch size (1.4)** Dev. class (0.9)*	#	Tree height (0.7)*	Age (3.0)***	#
Fic hyp	Patch size (32.0)*** Dev. class (1.4)***	Dev. class (3.8)*** Patch size (1.3)**	Patch size (9.3)*** Tree dom. (2.3)**	Age (2.7)***	Age (4.3)***	Tree height (2.4)***
Par mon	Patch size (17.2)*** Dev. class (3.2)***	Patch size (16.2)*** Dev. class (3.9)***	Patch size (43.5)*** Tree dom. (1.4)*	Tree height (3.3)***	Tree height (3.4)*** Tree species –(0.4)*	No model
Par cin	#	#	Patch size (20.8)***	#	#	Tree species –(1.1)*
Par cri	Patch size (24.7)*** Dev. class (3.9)***	Dev. class (5.7)*** Patch size (3.5)***	#	Tree diameter (4.1)***	Tree height (5.3)***	#
Par cae	Patch size (13.6)***	#	#	Age (1.7)*** Tree species (0.6)**	#	#
Par maj	Patch size (24.2)*** Tree dom. (0.7)*	Dev. class (4.0)*** Patch size (2.3)***	No model	Age (1.1)**	Age (2.7)***	Tree height (2.6)*** Age (1.2)*
Cer fam	Patch size (30.0)*** Dev. class (1.1)**	Dev. class (1.4)** Patch size (0.8)*	Patch size (11.6)***	Age (3.0)***	Age (3.4)*** Tree diameter –(0.9)** Tree height (0.3)*	No model
Per inf	#	No model	Patch size (5.4)***	#	No model	No model
Pyr pyr	Patch size (15.9)*** Dev. class (2.2)***	Patch size (5.4)*** Dev. class (4.6)***	Patch size (25.6)***	Age (1.8)***	Tree height (1.6)***	No model
Emb rus	Patch size (1.1)*	Patch size (2.2)*** Veg. class (1.1)**	Patch size (26.0)*** Tree dom. (1.7)*	Age (0.6)*	Tree species –(0.7)**	No model

Treecreeper (*Certhia familiaris*), Redstart, Mistle Thrush, Wood Warbler, Red-breasted Flycatcher and Pied Flycatcher increased with tree height. Increasing stand age positively affected the abundance of Wryneck, Great Spotted Woodpecker, Three-toed Woodpecker, Wren, Redstart, Mistle Thrush, Greenish Warbler, Chiffchaff, Red-breasted Flycatcher, Pied Flycatcher, Blue Tit, Great Tit, Treecreeper, Bullfinch and Rustic Bunting. Tree-species composition affected the abundance of five species studied. The Redstart, Willow Tit, Siberian Tit and Rustic Bunting were scarce in deciduous-dominated forests, whereas the Blue Tit preferred deciduous-dominated stands. Tree diameter was an important factor for Wren, Crested Tit and Treecreeper: this measure negatively affected Wren and Treecreeper abundances, and positively affected the Siberian Tit. In general, the importance of different explanatory factors varied considerably among regions.

4. Discussion

4.1. The composition and abundance of old-forest bird species in managed forests

The focal species were commonly observed in managed forests. Observed densities of, e.g., Great Woodpecker, Waxwing, Redstart, Siberian Tit and Siberian Jay correspond well with the densities observed in protected forest areas in Finland (Virkkala & Rajasärkkä 2007; Table 2). However, the managed forests supported lower densities of Three-toed Woodpecker, Wren, Greenish Warbler, Wood Warbler, Treecreeper and Rustic Bunting compared to protected forests. Based on the present and Virkkala & Rajasärkkä's (2007) data, we conclude that species that thrive in managed forests prefer pine-dominated forests, whereas species being scarce in managed forests prefer deciduous and/or spruce-dominated forests.

Our results also emphasize differences in old-forest bird assemblages between the southern and northern parts of the country. Some species were observed only in the north (Willow Grouse, Waxwing, Siberian Tit and Siberian Jay). These species have a general northerly distribution and they prefer coniferous forests (e.g., Väisänen *et al.* 1998). Other species, however, occurred solely in the

south (Wren, Greenish Warbler, Chiffchaff, Red-breasted Flycatcher, Crested Tit, and Blue Tit). These species show a southerly distribution and some prefer deciduous or mixed forests (e.g., Väisänen *et al.* 1998). Due to these differences, especially the habitat requirements of species associated with old coniferous forest should be considered in the managed forests in the north and those of deciduous-mixed forest species in the south. For the preservation of old-growth forest bird species, all boreal subzones and their zone-specific specialities must be considered both in reserve-network planning and in forest-management practices. Partly because the proportion of protected forests is higher in the north, the conservation situation of old-forest species appears better in northern than in southern Finland (Virkkala & Rajasärkkä 2007).

4.2. Importance of forest patch characteristics

According to our results, forest-patch size and development class were the most important forest-patch characteristics explaining the abundance of old-forest birds in managed forests. Virkkala and Rajasärkkä (2006) noted that the mean density of species preferring old-growth forests was significantly higher in the large than in the small old-growth forest patches in the north-boreal zone in Finland. Especially Hazel Grouse, Three-toed Woodpecker, Redstart, Mistle Thrush, Chiffchaff, Pied Flycatcher, various *Parus* species, Treecreeper, Bullfinch, and Rustic Bunting were sensitive to patch size. For these species $\geq 20\%$ of variation in the abundance was explained by patch size in at least one study region. These results generally corroborate earlier community-level studies done in Finland (Virkkala *et al.* 1994, Raivio 1992, Jokimäki & Huhta 1996, Virkkala 1996) as well as species-specific studies conducted, for instance, with the *Picoides* species (Fayt 2003, Roberge & Angelstam 2006, Gagne *et al.* 2007), Siberian Tit (Virkkala & Liehu 1990) and Treecreeper (Kuitunen & Helle 1988, Suorsa *et al.* 2005). Generally, food abundance decreases with decreasing patch size (Burke & Nol 1998, Zanette *et al.* 2000; but see Jokimäki *et al.* 1998), possibly affecting the nutritional and physiological-stress conditions of adults and the condition of nestlings (Huhta *et al.*

1999, Suorsa *et al.* 2003) for individuals living in small patches or at forest edges. In addition, in small-sized forest patches surrounded by inhospitable matrix for species, individuals are forced to use suboptimal foraging areas (Kuitunen 1987, Kuitunen & Mäkinen 1993, Huhta *et al.* 1999).

In this paper, we did not study the effects of forest fragmentation on bird species *per se*. Fragmentation negatively affects many northern taiga species, such as Three-toed Woodpecker, Siberian Tit and Rustic Bunting (Helle 1985a, Virkkala 1987a, Raivio & Haila 1990, Jokimäki & Huhta 1996). Eight of the patch-size sensitive species in our study were cavity nesters. Indeed, Virkkala *et al.* (1994) reported a positive correlation between the size of old-growth forest patches and the density of cavity nesters. In Kainuu, northern Finland, Three-toed Woodpecker, Treecreeper and Crested Tit have peak densities in the largest old-growth forest areas (Virkkala 1996). Similarly, in northern Sweden, habitat generalists occupy all forest size classes, whereas species requiring specific characteristics of forests avoided forest patches <5 ha in size, regardless of landscape composition (Edenius & Sjöberg 1997).

The succession from sapling to mature stands (the factor development class in our models) positively affected the old-forest species in the south and east but not in the north. Part of this geographical variation might be related to the matrix that is more forested in the north than in the other study regions. Many of these species were resident cavity nesters, such as woodpeckers, tits and Treecreeper, but also migrants such as Redstart and *Ficedula* flycatchers. The importance of old forests for residents and cavity nesters has been demonstrated in earlier (e.g., Järvinen *et al.* 1977, Helle 1985b). The densities of many cavity-nesting birds have decreased due to forest management (Haapanen 1965, Helle 1985b, Virkkala *et al.* 1994). According to Imbeau *et al.* (2001), the most sensitive bird species for forestry both in Fennoscandian and Eastern Canadian boreal forests are resident cavity-nesters. An obvious reason is the lack of suitable nesting trees in managed forests. For resident species, old forests may be more favourable than managed forests also in winter, as they may host more invertebrate prey (Pettersen *et al.* 1995). We suggest that large mature and old-growth forest stands are particularly

important for resident forest birds especially during winter months. Mixed tree-species composition appears beneficial for old-forest birds (Jokimäki & Huhta 1996). However, vegetation class did not seem to be an important factor affecting old forest bird species, although Hazel Grouse, Chiffchaff, *Ficedula* species, Willow Tit, Great Tit and Rustic Bunting showed some preference towards mixed-wood forests.

4.3. The importance of tree characteristics within forest patch

Stand age and tree height were the most important tree characteristics affecting the habitat occupancy of old-forest bird species, whereas tree-species composition and tree diameter were of minor importance here. Because stand age and tree height correlated positively with each other, the abundance of several species such as the Great Spotted Woodpecker, Bullfinch, Treecreeper, Redstart and Pied Flycatcher correlated positively with both of these variables. All species that benefited from increasing stand age and tree height were cavity nesters (except Bullfinch). The effects of stand age and tree height cannot be reliably distinguished because of the intercorrelation; an old-forest stand also offers more suitable trees for cavity-nesting species than a younger stand (Haapanen 1965, 1966). The important role of stand age for forest-bird richness, and especially for cavity nesters, has earlier been reported in northern Finland (Jokimäki & Huhta 1996).

Although Helle (1985b) and Virkkala (1987b) reported a positive relationship between forest-bird density and timber volume in northern coniferous forests, tree diameter (that presumably positively correlates with timber volume) was seldom included in the habitat–abundance models of bird species considered in the present study. Apparently stand age partly masked the role of timber volume in the present data, or *vice versa* (see also Jokimäki & Huhta 1996). In general, increasing stand age, timber volume and tree height all indicate a high overall productivity of such stands that might be beneficial to birds living in managed forests (see Honkanen *et al.* 2010). It must be noted that both the number of trees as well as their size affect timber volume in a forest patch. Normally,

tree density is higher in natural than managed old forests. It must be noted that the tree-species composition variable was categorical, and therefore its resolution was lower than the resolution of continuous variables (stand age and tree height, and tree diameter). Therefore, it can be expected to appear slightly less important than the other variables. Indeed, our analyses using general forest-patch variables indicated the important role of tree-species dominance for some species.

The Redstart, Willow Tit, Siberian Tit and Rustic Bunting preferred patches with coniferous trees (see also Haapanen 1965). For *Parus* species, coniferous trees offer more food during winter than do deciduous trees. In addition, Siberian Tits prefer coniferous over deciduous trees also during nesting and fledgling periods (Virkkala 1988) despite insect fauna being richer in birch than in coniferous trees during summer (Palmgren 1932). Because selection of different tree species in forest management may play an important role in conservation of old-growth forest species, the best solution for old-forest bird species might be mixed-tree species composition. The significant negative effect of tree diameter on the abundance of Tree-creeper was surprising, considering that the species particularly forages on large-diameter trunks (Suorsa *et al.* 2005; see also Aho *et al.* 2010). This result could be partly explained by the positive correlation between tree diameter and stand age, as well as the presumably higher density of trees in natural than in managed old forests. Unfortunately, our data for the Treecreeper were too small to study the effects of these variables separately.

Although the present forest data had been collected at a single spatial scale (the forest patch), general forest patch variables (patch size, development class, vegetation class and tree dominance) and the variables describing trees within a patch (tree species, stand age, tree height and tree diameter) might have biologically different importance for the focal species (Jokimäki & Huhta 1996). Our results indirectly support the hypothesis by Jokimäki and Huhta (1996) that for species with a strict requirement for old forest habitat, forest patch-level factors such as tree age are more important than are large-scale matrix factors. However, for managed-forest bird species, matrix-level factors such as forest fragmentation or edge effects might be more important (positive) factors. For

some resident old-forest species, very large old forests are required for conservation (Virkkala 1987a, 1991).

4.4. Methodological considerations

We used 1 km × 1 km study plots that have been applied in the Finnish summer atlas (Pakkala & Väisänen 2000, 2001). Our earlier work found that this method is an effective way to collect data on relatively rare species living in managed forests in Finland (Solonen & Jokimäki 2011). For practical reasons (three visits, several study plots and multiple study species), the use of larger study plots was not feasible. Most of the focal species were small passerines with territory sizes often only up to a few ha, and we suppose that 1 km × 1 km study plots were suitable to study their habitat requirements. However, larger study plots might have been better to study habitat associations of species with larger territories, such as the Three-toed Woodpecker, Siberian Tit and Siberian Jay. In addition, we studied habitat associations in summer months only. It is probable that resident bird populations are limited by winter survival, and therefore they may require larger areas in winter than in summer (Kuitunen & Helle 1988, Pechacek 2004).

4.5. Conclusions

Our results suggest that forest characteristics affect the occurrence of old forest birds in a species-specific way (Jokimäki & Huhta 1996, Elmberg & Edenius 1999), although patch size was important for most species. In addition, different factors may affect bird-species abundance in different regions. Therefore, conservation measures of these species in managed forested landscapes should be both species- and region-specific. However, in practice, management of very large areas may not be possible in a species-specific manner. In addition, because of complex, season-specific requirements, resident species may require high-diversity forest landscapes. Moreover, many old-forest bird species, especially those preferring pine-forests, thrive in commercially-used forests if large-sized old-forest patches are retained in the landscape.

Patch size, development class, stand age and tree height were among the most important factors in explaining the abundance of old-forest bird species densities in commercially-used forests. These stand features seem to be especially important for residents and cavity nesters. However, the forest characteristics used as explanatory variables are probably seldom of primary importance for birds as such but rather indicate the availability of some essential resources related to food supply, nesting opportunities, or cover.

Although the forest-inventory data used here lack some variables that are surely important for the birds, such as the occurrence of tree cavities, they explained variation in the old-forest bird abundances rather well. Therefore, integrating the national bird-monitoring and forest-inventory data is a promising way to obtain more information about the bird-habitat relationships across large spatial scales in commercially-used forest landscapes (Edenius & Mikusiński 2006, Fearer *et al.* 2007, St-Laurent *et al.* 2007, Venier & Pearce 2007).

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Vanhon metsien lintulajien elinympäristövaatimukset borealisissa metsissä

Suojelualueet ovat tärkeitä useille vanhoja metsiä vaativille lajeille, mutta useimpia näistä lajeista tavataan talousmetsissäkin. Teimme kolmen kieroksen pesimälinnustokartoituksen 37:llä talousmetsiin sijoitetulla 1 km² ruudulla ja käytimme Valtakunnallisen Metsien Inventoinnin (VMI) aineistoa selvittääksemme 23 vanhojen metsien lintulajien elinympäristövaatimuksia kolmella alueella: Etelä-, Itä- ja Pohjois-Suomessa. Havaituista 23 kohdelintulajista 12 havaittiin kaikilla alueilla, määrän vaihdellessa alueittain 16–21 lajin välillä. Lintujen kokonaisparimäärä ei vaihdellut merkit-

sevästi alueiden välillä, toisin kuin useiden yksittäisten lajien määrät. Metsälaikun kasvava koko oli tärkein tekijä, vaikuttaen positiivisesti suurimpaan osaan tarkasteltuja lajeja. Metsän kehitysluokka vaikutti valtaosaan lajeista etelässä ja idässä; yleisemmin varttuneisiin ja vanhoihin metsiin sopeutuneisiin lajeihin. Metsikön valtuuoston korkeus ja ikä esiintyivät parhaissa malleissa useammin kuin puulaji ja puiden rinnankorkeuslääpimitta.

Yleisesti ottaen metsikön koko, kehitysluokka, valtuuoston ikä ja korkeus olivat merkittävimpiä vanhojen metsien lintulajien runsauden selittäjiä tutkituissa talousmetsissä. Nämä rakennepiirteet olivat erityisen tärkeitä paikkalintu- ja kolopesijälajeille. Tuloksemme viittaavat siihen, että vanhojen metsien lintulajien vasteet talousmetsämaiseman vaihteluun ovat lajikohtaisesti erilaisia, ja että eri alueilla lajeihin voivat vaikuttaa eri tekijät. Käytetty VMI-aineisto selitti hyvin tutkittujen vanhojen metsien lajien runsautta. Lintukartoitustietojen ja VMI:n metsälaikkutietojen yhdistäminen tarjoaa erinomaisen mahdollisuuden selvittää metsälintujen elinympäristövaatimuksia ja kuvata metsätalouden vaikutuksia linnustoon metsätalouden omalla kielellä.

References

- Aho, T., Kuitunen, M., Suhonen, J. & Jäntti, A. 2010: Determination of clutch size in treecreepers *Certhia familiaris* under food and time constraints. — *Ornis Fennica* 87: 77–92.
- Andrén, H. 1994: Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. — *Oikos* 71: 355–366.
- Barbault, R. & Sastrapradja, S.D. 1995: Generation, maintenance and loss of biodiversity. — In *Global Biodiversity Assessment* (ed. Heywood, W.H.): 193–274. Cambridge Univ. Press, Cambridge.
- Bellamy, P.E., Hinsley, S.A. & Newton, I. 1996: Factors influencing bird species numbers in small woods in south-east England. — *Journal of Applied Ecology* 33: 249–262.
- Bibby, C.J., Burgess, N.D. & Hill, D.A. 1992: Bird census techniques. — Academic Press, London.
- Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A. & Rajasärkkä, A. 2003: Effects of landscape structure and forest reserve location on old-growth forest bird species in northern Finland. — *Landscape Ecology* 18: 377–393.
- Burke, D.M. & Nol, E. 1998: Influence of food abundance,

- nest-site habitat, and forest fragmentation on breeding Ovenbirds. — *Auk* 115: 96–104.
- Edenius, L. & Elmberg, J. 1996: Landscape level effects of modern forestry on bird communities in North Swedish boreal forests. — *Landscape Ecology* 11: 325–338.
- Edenius, L. & Mikusiński, G. 2006: Utility of habitat suitability models as biodiversity assessment tools in forest management. — *Scandinavian Journal of Forest Research* 21: 62–72.
- Edenius, L. & Sjöberg, K. 1997: Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. — *Ecography* 20: 425–431.
- Elmberg, J. & Edenius, L. 1999: Abundance patterns in bird communities in old boreal forests in relation to stand structure and local habitat configuration. — *Ornis Fennica* 76: 123–133.
- Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997: Boreal forests. — *Ecological Bulletins* 46: 16–47.
- Fayt, P. 2003: Population ecology of the three-toed woodpecker under varying food supplies. — Ph.D. thesis, University of Joensuu. 126 pp.
- Fearer, T.M., Prisley, S. P., Stauffer, D.F. & Keyser, P.D. 2007: A method for integrating the breeding bird survey and forest inventory and analysis databases to evaluate forest bird–habitat relationships at multiple spatial scales. — *Forest Ecology and Management* 243: 128–143.
- Forman, R.T.T. & Godron, M. 1986: *Landscape Ecology*. — Wiley, New York.
- Fuller, R.J., Smith, K.W., Grice, P.V., Currie, F.A. & Quine, C.P. 2007: Habitat change and woodland birds in Britain: implications for management and future research. — *Ibis* 149 (suppl. 2): 261–268.
- Gagne, C., Imbeau, L. & Drapeau, P. 2007: Anthropogenic edges: Their influence on the American three-toed woodpecker (*Picoides dorsalis*) foraging behaviour in managed boreal forests of Quebec. — *Forest Ecology and Management* 252: 191–200.
- Gustafsson, E. J. & Parker, G. R. 1992: Relationships between landcover proportion and indices of landscape spatial pattern. — *Landscape Ecology* 7: 101–110.
- Gärdenfors, U. (ed.) 2005: The 2005 red list of Swedish species. — Uppsala, ArtDatabanken, SLU.
- Haapanen, A. 1965: Bird fauna of the Finnish forests in relation to forest succession. I. — *Annales Zoologici Fennici* 2: 153–196.
- Haapanen, A. 1966: Bird fauna of the Finnish forests in relation to forest succession. II. — *Annales Zoologici Fennici* 3: 176–200.
- von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–1972: *Pohjolan linnut värikuvien*. — Otava, Helsinki.
- Helle, P. 1985a: Effects of forest fragmentation on bird densities in northern boreal forests. — *Ornis Fennica* 62: 35–41.
- Helle, P. 1985b: Effects of forest regeneration on the structure of bird communities in northern Finland. — *Holarctic Ecology* 8: 120–132.
- Honkanen, M., Roberge, J.M., Rajasärkkä, A. & Mönkkönen, M. 2010: Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. — *Global Ecology and Biogeography* 19: 61–71.
- Huhta, E., Jokimäki, J. & Rahko, P. 1999: Breeding success of Pied Flycatchers in artificial forest edges: the effects of a suboptimally shaped foraging area. — *Auk* 116: 528–535.
- Imbeau, L., Mönkkönen, M. & Desrochers, A. 2001: Long-term effects of forestry on birds of the eastern Canadian boreal forests: a comparison with Fennoscandia. — *Conservation Biology* 15: 1151–1162.
- Jansson, G. 2001: Övervakningssystem för skogens fåglar — uppföljning av naturvårdsarbetet. — Världsnaturfonden WWF, Solna. (In Swedish)
- Janzen, D.H. 1983: No park is an island: increase in interference from outside as park size decreases. — *Oikos* 41: 402–410.
- Jokimäki, J. & Huhta, E. 1996: Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. — *Ornis Fennica* 73: 97–113.
- Jokimäki, J., Huhta, E., Itämies, J. & Rahko, P. 1998: Distribution of arthropods in relation to forest patch size, edge and stand characteristics. — *Canadian Journal of Forest Research* 28: 1068–1072.
- Järvinen, O., Kuusela, K. & Väisänen, R.A. 1977: Effects of modern forestry on the number of breeding birds in Finland. — *Silva Fennica* 11: 284–294. (In Finnish with English summary)
- Järvinen, O. & Lokki, J. 1978: Indices of community structure in bird censuses based on a single visit: effects of variation in species efficiency. — *Ornis Scandinavica* 9: 87–93.
- Järvinen, O. & Väisänen, R.A. 1978: Recent changes in forest bird populations in northern Finland. — *Annales Zoologici Fennici* 15: 279–289.
- Järvinen, O. & Väisänen, R.A. 1979: Changes in bird populations as criteria of environmental changes. — *Holarctic Ecology* 2: 75–80.
- Kissling, M.L. & Garton, E.O. 2006: Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. — *Auk* 123: 735–752.
- Koskimies, P. & Väisänen, R. A. 1991: *Monitoring bird populations: a manual of methods applied in Finland*. — University of Helsinki, Helsinki.
- Kouki, J. & Väänänen, A. 2000: Impoverishment of resident old-growth forest bird assemblages along isolation gradient of protected areas in eastern Finland. — *Ornis Fennica* 77: 145–154.
- Kuitunen, M. 1987: Seasonal and geographical variation in the clutch size of the Common Treecreeper *Certhia familiaris*. — *Ornis Fennica* 64: 125–136.

- Kuitunen, M. & Helle, P. 1988: Relationship of the common treecreeper (*Certhia familiaris*) to edge effect and forest fragmentation. — *Ornis Fennica* 65: 150–155.
- Kuitunen, M. & Mäkinen, M. 1993: An experiment in nest site choice of the common treecreeper in fragmented boreal forests. — *Ornis Fennica* 70: 163–167.
- McLellan, C.H., Dobson, A.P., Wilcove, D.S. & Lynch, J.F. 1986: Effects of forest fragmentation on New- and Old-World bird communities: empirical observations and theoretical implications. — In *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates* (eds. Verner, J., Morrison, M.L. & Ralph, C.J.): 305–313. University Wisconsin Press, Madison.
- Mönkkönen, M., Huhta, E., Mäkelä, J. & Rajasärkkä, A. 2000: Effects of forest fragmentation on bird assemblages in northern Finnish old forest reserves, Oulanka-Paanajärvi area as a reference. — *Linnut-vuosikirja* 1999: 91–97. (In Finnish with English summary)
- Opdam, P. 1991: Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. — *Landscape Ecology* 5: 93–106.
- Pakkala, T. & Väisänen, R.A. 2000: A new method for local bird atlas surveys in 1-km grid squares during summer and winter. — *Linnut* 35(1): 6–11. (In Finnish with English summary)
- Pakkala, T. & Väisänen, R.A. 2001: Lintujen kesäatlasten kartoitusohjeet. — Photocopy, Helsingin yliopiston eläinmuseo, Helsinki. (In Finnish)
- Palmgren, P. 1932: Zur Biologie von *Regulus r. regulus* und *Parus atricapillus borealis* Selys. — *Acta Zoologica Fennica* 14: 1–113.
- Pechacek, P. 2004: Spacing behavior of Eurasian three-toed woodpecker (*Picoides tridactylus*) during the breeding season in Germany. — *Auk* 121: 58–69.
- Pettersen, R.B., Ball, J.P., Renhorn, J.P., Esseen, P.-A. & Sjöberg, K. 1995: Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. — *Biological Conservation* 74: 57–63.
- Raivio, S. 1992: Bird communities in fragmented coniferous forests: the importance of quantitative data and adequate scaling. — Ph.D. thesis, Department of Zoology, University of Helsinki.
- Raivio, S. & Haila, Y. 1990: Bird assemblages in silvicultural habitat mosaics in southern Finland during the breeding season. — *Ornis Fennica* 67: 73–83.
- Rassi, P., Alanen, A., Kanerva, T. & Mannerkoski, I. 2001: The 2000 red list of Finnish species. — *Ympäristöministeriö & Suomen ympäristökeskus*, Helsinki. (In Finnish with English summary)
- Roberge, J.-M. & Angelstam, P. 2006: Indicator species among resident forest birds — A cross-regional evaluation in northern Europe. — *Biological Conservation* 130: 134–147.
- Saab, V. 1999: Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. — *Ecological Applications* 9: 135–151.
- Schmiegelow, F.K.A., Machtans, C.S. & Hannon, S.J. 1997: Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. — *Ecology* 78: 1914–1932.
- Solonen, T. & Jokimäki, J. 2011: The efficiency of three-visit square surveys vs. one-visit line transects in censusing sparsely distributed birds in managed forest landscapes. — *Bird Conservation International* 21: 156–171.
- SPPS Inc. 2006. SPSS 15.0. Command Syntax Reference. — SPPS Inc., Chicago, IL.
- St-Laurent, M.-H., Ferron, J., Hins, C. & Gagnon, R. 2007: Effects of stand structure and landscape characteristics on habitat use by birds and small mammals in managed boreal forest of eastern Canada. — *Canadian Journal of Forest Research* 37: 1298–1309.
- Suorsa, P., Huhta, E., Jäntti, A., Nikula, A., Helle, H., Kuitunen, M., Koivunen, V. & Hakkarainen, H. 2005: Thresholds in selection of breeding habitat by the Eurasian treecreeper (*Certhia familiaris*). — *Biological Conservation* 121: 443–452.
- Suorsa, P., Huhta, E., Nikula, A., Nikinmaa, M., Jäntti, A., Helle, H. & Hakkarainen, H. 2003: Forest management is associated with physiological stress in an old-growth forest passerine. — *Proceedings of the Royal Society of London Ser. B* 270: 963–969.
- Systat Inc. 2004: SigmaStat 3.1. User's manual. — Systat Software, Point Richmond, CA.
- Venier, L.A. & Pearce, J.L. 2007: Boreal forest landbirds in relation to forest composition, structure and landscape: implications for forest management. — *Canadian Journal of Forest Research* 37: 1214–1226.
- Villard, M.-A., Kurtis Trzcinski, M. & Merriam, G. 1999: Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. — *Conservation Biology* 13: 774–783.
- Virkkala, R. 1987a: Effects of forest management on birds breeding in northern Finland. — *Annales Zoologici Fennici* 24: 281–294.
- Virkkala, R. 1987b: Geographical variation in bird communities of old, intact forest in northern Finland. — *Ornis Fennica* 64: 108–118.
- Virkkala, R. 1988: Foraging niches of foliage-gleaning birds of old, intact forest in northern Finland. — *Ornis Fennica* 65: 104–113.
- Virkkala, R. 1991: Population trends of forest birds in a Finnish Lapland landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? — *Biological Conservation* 56: 223–240.
- Virkkala, R. 1996: Reserve network in Finland and the need for developing the network: an ecological approach. — Finnish Environment Research, Nature and Land Use Division. 53 pp. (In Finnish with English summary)
- Virkkala, R. 2000: Population dynamics of breeding birds in a managed south-boreal forest area. — In *Distur-*

- bance dynamics in boreal forests (eds. Karjalainen, L. & Kuuluvainen, T.): 157. Yliopistopaino, Helsinki.
- Virkkala, R., Korhonen, K. T., Haapanen, R. & Aapala, K. 2000: Protected forests and mires in forest and mire vegetation zones in Finland based on the 8th National Forest Inventory. — *Finnish Environment* 395: 1–49. (In Finnish with English summary)
- Virkkala, R. & Liehu, H. 1990: Habitat selection by the Siberian tit *Parus cinctus* in virgin and managed forests in northern Finland. — *Ornis Fennica* 67: 1–12.
- Virkkala, R. & Rajasärkkä, A. 2001: The role of protected areas in preserving forest and mire bird populations. — *Linnut-vuosikirja* 2000: 34–43. (In Finnish with English summary)
- Virkkala, R. & Rajasärkkä, A. 2006: Spatial variation of bird species in landscapes dominated by old-growth forests in northern boreal Finland. — *Biodiversity and Conservation* 15: 2143–2162.
- Virkkala, R. & Rajasärkkä, A. 2007: Uneven regional distribution of protected areas in Finland: Consequences for boreal forest bird populations. — *Biological Conservation* 134: 361–371.
- Virkkala, R., Rajasärkkä, A., Väisänen, R.A., Vickholm, M. & Virolainen, E. 1994: Conservation value of nature reserves: do hole-nesting birds prefer protected areas in southern Finland? — *Annales Zoologici Fennici* 31: 173–186.
- Väisänen, R.A., Järvinen, O. & Rauhala, P. 1986: How are extensive, human-caused habitat alterations expressed on the scale of local bird populations in boreal forests? — *Ornis Scandinavica* 17: 282–292.
- Väisänen, R.A., Lammi, E. & Koskimies, P. 1998: Distribution, numbers and population changes of Finnish breeding birds. — *Otava*, Helsinki. (In Finnish with English summary)
- Wilcove, D.S., McLellan, C.H. & Dobson, A.P. 1986: Habitat fragmentation in temperate zone. — In *Conservation biology: the science of scarcity and diversity* (ed. Soulé, M.E.): 237–256. Sinauer, Sunderland, MA.
- Zanette, L., Doyle, P. & Trémont, S.M. 2000: Food shortage in small fragments: evidence from an area-sensitive passerine. — *Ecology* 81: 1654–1666.
- Zar, J. H. 1984: *Biostatistical Analysis*. — Prentice-Hall, Englewood Cliffs, NJ.